How to Find one’s Way in the Labyrinth of Path Integration Models

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Several models have been developed to explain how an animal can process route-based information to memorize its home location, i.e. the starting point of its outward path. This ability was hypothesized early on as a kind of dead-reckoning (Darwin, 1873). It is now usually described as path integration (Mittelstaedt & Mittelstaedt, 1980) or route-based navigation (Baker, 1981). From the animal’s point of view, memorizing the home location on the basis of route-based information is likely to be an egocentric coding process (Potegal, 1972, 1982). Consequently, path integration should be thought of as a mechanism which enables the moving animal to update the egocentric vector specifying the head-referred direction ($\omega$) and the distance ($D$) to the memorized home location. Path integration models, however, have been developed with different purposes (see Maurer & Séguidot, 1995), using considerably different types of formalism that make their predictions difficult to compare. The aim of this paper is simply to provide a comprehensive view of these models in reformulating them, whenever possible, in common egocentric terms.

Although an animal’s movement is usually a continuous process, it is useful to represent the animal’s outward path as a sequence of steps (translations) alternating with changes of direction (rotations; see Bovet & Benhamou, 1988). Path integration as an updating mechanism is then described by recurrent formulas by which the egocentric vector specifies the memorized home location after $n$ + 1 steps ($\omega_{n+1}; D_{n+1}$) as a function of its previous value computed after $n$ steps ($\omega_n; D_n$). The route-based information used by the updating mechanism is provided by the measures of the last change of direction ($\alpha_n$) and of the last step length ($P_{n+1}$) the animal has made.

Models are presented in chronological order. The variables involved are described in Fig. 1. The meaning of symbols and the mathematical expressions of the models rewritten with egocentric recurrent formulas are given in Table 1. The $X$-axis is arbitrarily chosen as the reference direction used to compute the direction of the animal’s location from home ($\Phi$) and the animal’s moving direction (i.e. step orientation $\theta$). All angular values are expressed in radians ($180^\circ = \pi$ rad).

Model 1 was proposed by Jander (1957), who assumed that the direction of the animal’s location from home could be expressed as the time-weighted angular mean of moving directions: $\Phi_n = \sum_{i=1}^n t_i \theta_i / \sum_{i=1}^n t_i$, where $t_i$ is the time spent moving in direction $\theta_i$. Assuming a constant speed, this equation can be rewritten $\Phi_n = \sum_{i=1}^n P_i \theta_i / L_n$, hence: $\Phi_{n+1} = (L_n \Phi_n + P_{n+1} \theta_{n+1}) / L_{n+1} = \Phi_n + \delta_n P_{n+1} / L_{n+1}$, with $\delta_n$ expressed between $-\pi$ and $+\pi$ rad. The head-referred direction of the memorized home location can then be easily expressed in a recurrent form [Table 1, eqn (1)].

Model 2 was developed by Mittelstaedt & Mittelstaedt (1973, 1982), who expressed the vector specifying the direction and distance to the animal’s location from home after $n$ steps on the basis of the Cartesian coordinates of this location $X_n = \sum_{i=1}^n P_i \cos(\theta_i) + X_0$ and $Y_n = \sum_{i=1}^n P_i \sin(\theta_i) + Y_0$: $\Phi_n = \arctan[(Y_n - Y_0)/(X_n - X_0)] + b\pi$ and $D_n = [(X_n - X_0)^2 + (Y_n - Y_0)^2]^{1/2}$, with $b = 0$ if $(X_n - X_0) > 0$ and 1 otherwise. Unfortunately, there is no simple means to provide egocentric recurrent formulas.
Table 1

Meaning of symbols and egocentric recurrent formulas

<table>
<thead>
<tr>
<th>Model</th>
<th>Formula</th>
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<tbody>
<tr>
<td>1</td>
<td>$\omega_{n+1} = (\omega_n - \omega_x) + (\alpha \pi - \omega_x) \psi_{n+1}/L_{n+1}$</td>
</tr>
<tr>
<td>2</td>
<td>(approx.) $\Phi = \arctan(Y_n - Y_0)/(X_n - X_0)$ + $b\pi$ (no egocentric recurrent formula)</td>
</tr>
<tr>
<td></td>
<td>(right) $D_n = [(X_n - X_0)^2 + (Y_n - Y_0)^2]^{1/2}$ (no egocentric recurrent formula)</td>
</tr>
<tr>
<td>3</td>
<td>(approx.) $\omega_{n+1} = (\omega_n - \omega_x) + k(\omega_n - \omega_x)(2\pi - \omega_n + \omega_x)/(\pi)$</td>
</tr>
<tr>
<td></td>
<td>(right) $D_{n+1} = D_n + \psi_{n+1}(1 - 2</td>
</tr>
<tr>
<td>4</td>
<td>$\omega_{n+1} = \arctan\sin(\omega_n - \omega_x)/(\cos(\omega_n - \omega_x) - P_{n+1}/D_n) + b\pi$</td>
</tr>
<tr>
<td></td>
<td>(right) $D_{n+1} = [D_n^2 + P_{n+1}^2 - 2D_n P_{n+1}\cos(\omega_n - \omega_x)]^{1/2}$</td>
</tr>
<tr>
<td>5</td>
<td>(approx.) $\omega_{n+1} + \sin(\omega_n - \omega_x) P_{n+1}/D_n$</td>
</tr>
<tr>
<td></td>
<td>(right) $D_{n+1} = D_n + P_{n+1}\cos(\omega_n - \omega_x)$</td>
</tr>
</tbody>
</table>

$\delta = \Phi_{n+1} - \Phi n = \pm \pi - (\omega_n - \omega_x)$: angle by which the \((n+1)\)-th step direction deviates from $\Phi$ [with $a = 1$ if $(\omega_n - \omega_x)$ expressed between $-\pi$ and $+\pi$ is positive and $a = -1$ otherwise (Models 1 and 3), and $b = 0$ if the denominator is positive and 1 otherwise (Models 2 and 4).]

$X_n, Y_n$: coordinates of the animal’s location after $n$ steps ($X_0, Y_0$: home location).

$\Phi_n$: direction of the animal’s location from home after $n$ steps.

$\psi_n$: direction of the memorized home location after $n$ steps.

$P_0, \theta$: length and orientation of the $n$-th step.

$\omega_n$: head-referred direction of the animal's location after $n$ steps.

$D_n$: beeline distance to the memorized home location after $n$ steps.

$X_0, Y_0$: coordinates of the animal's location after $n$ steps.

Model 3 was developed by Müller & Wehner (1988) from Model 1. Initially, it dealt with steps of one unit length. The version given here is generalized for a step length $P$ which may differ from one. Müller & Wehner (1988) assumed that the direction of the animal’s location from home could be recurrently computed in an approximate (rather than exact) form: $\Phi_{n+1} = (D_n \Phi_n + P_n \theta_n)/(D_n + P_n), \Phi_n + \delta_n P_n + (D_n + P_n)$, with $\delta_n$ expressed between $-\pi$ and $+\pi$ rad. This equation was later slightly simplified (assuming $D_n$ large): $\Phi_{n+1} = \Phi_n + \delta_n P_n + D_n$. As the systematic errors predicted by this equation did not fit well with those actually made by ants after a two-leg constrained outward path, Wehner & Müller (1988) proposed the following empirically modified equation: $\Phi_{n+1} = \Phi_n + k(\pi - \delta_n)(\pi + \delta_n)\delta_n + D_n$, with $k = 0.132$ rad$^{-2}$ ensuring the angular product to maximally reach $\pi/2$ rad. On the other hand, the distance from home was also recurrently computed in an approximate form: $D_{n+1} = D_n + P_n(1 - 2|\delta_n|/\pi)$. The direction and distance to the memorized home location can then be easily expressed using egocentric recurrent formulas [Table 1, eqns (3a, b)].

Model 4 was developed by Benhamou et al. (1990) to study the efficiency of the egocentric coding process against random errors on route-based information. After $n+1$ steps the Cartesian coordinates of the home location, expressed in a system of reference (X', Y') centred on the animal’s location with the X'-axis corresponding to the body-head axis, are: $X_{n+1}' = D_n \cos(\omega_n - \omega_x) - P_{n+1}$ and $Y_{n+1}' = D_n \sin(\omega_n - \omega_x)$. The egocentric coding of the memorized home location is therefore expressed recurrently simply as $\omega_{n+1} = \arctan(Y_{n+1}' / X_{n+1}') + b\pi$ and $D_{n+1} = (X_{n+1}'^2 + Y_{n+1}'^2)^{1/2}$, with $b = 0$ if $X_{n+1}' > 0$ and 1 otherwise [Table 1, eqns (4a, b)].

Model 5 was presented by Gallistel (1990). It deals with the egocentric coding process based on a continuous (rather than discrete) updating mechanism. The animal’s movement was considered as a continuous curve, and path integration was then
described by differential equations. Unfortunately, the published formulas are wrong (although they are given as being correct). The correct formulas are: \( \frac{d\omega}{dt} = -\frac{d\theta}{dt} + \frac{ds}{dt} \sin(\omega) \) and \( \frac{d\theta}{dt} = -\frac{dx}{dt} \cos(\omega) \), where \( t \) is the time and \( s \) the curvilinear abscissa \( (ds/dt: \text{animal’s linear speed}; d\theta/dt: \text{animal’s angular speed}) \).

If the animal’s movement is now taken to be a discrete step process, the egocentric coding of the memorized home location can be easily approximated by recurrent formulas [Table 1, eqns (5a, b)].

**Comments**

Four models out of five (1, 3, 4 and 5) are liable to provide recurrent formulas specifying the head-referred direction of the memorized home location. This direction \( (\omega_{n+1} \text{ after } n+1 \text{ steps}) \) always depends on two terms. The first term, similar in the four models \( (\omega_{n} - \omega_{c}) \), is simply the consequence of the animal’s last rotation \( (\omega_{c}) \). The second term, varying from model to model, is the consequence of the animal’s subsequent translation \( (P_{n+1}) \). The four models therefore differ mainly in the way the virtual motion parallax of the memorized home location is managed during animal’s translations. Three models (3, 4 and 5) can also provide recurrent formulas specifying the distance between the animal and its home.

Jander (1957) believed that his formulation (Model 1) was mathematically correct, but it is not: in numerous situations, it entails a considerable systematic error (see Wehner & Wehner 1986). The correct formulas are provided by Model 4. Model 2 is also mathematically correct, but it is of limited interest because it cannot be reformulated in egocentric terms. Model 5 is useful in providing the right solution for continuous updating. Furthermore, eqns (5a) and (5b) reliably approximate the correct eqns (4a) and (4b) for discrete step movements when the ratio \( P_{n+1}/D_{a} \) is small.

Model 3 is deliberately based on approximate formulas, because Müller & Wehner (1988) developed it to account for systematic errors made by ants in estimating the home direction in some conditions (see also Séguinot et al., 1993). These authors modified the time-weighted angular mean formula (Model 1) by giving less weight to the past (using \( D_{l} \) instead of \( L_{l} \)), to improve the goodness-of-fit between the systematic errors provided by the formula and the data. It is amazing to notice that, in doing so and after other ad hoc modifications, they found an approximate angular formula which proves to have a partially correct structure when rewritten in egocentric terms [compare eqns (3a) and (5a)]; the rotation effect is embodied in the difference \( \omega_{n} - \omega_{c} \), and the translation effect is proportional to the ratio \( P_{n+1}/D_{a} \), and is set to 0 when \( (\omega_{n} - \omega_{c}) \) is equal to 0 or \( \pm \pi \) rad. It is eventually simpler to slightly modify a right formula to make it produce systematic errors. Thus, multiplying the ratio \( P_{n+1}/D_{a} \) with a constant \( c = 1.6 \) in eqns (4a) or (5a) may account for the systematic errors observed by Müller & Wehner (1988). In this framework, systematic errors are taken to be due to an overestimation of the translation effect \( (c>1) \) in estimating the home direction.

Gallistel (1990) erroneously claimed that the egocentric formulation of path integration is computationally unattractive because of its error-amplifying properties. Actually, computer simulations based on Model 4 have shown that random estimation errors in step lengths and in changes of direction when allotheticall measured (i.e. with reference to a compass direction) entail only a limited resultant random error in the egocentrically memorized home location; only random estimation errors in changes of direction when idiothetically measured (i.e. on the basis of endogenous movement-related information) entail a considerable resultant random error (Behamou et al., 1990). In accordance with these results, hamsters, which measure their rotations mainly from vestibular information, are completely lost after a few turns (Etienne et al., 1988), whereas ants, which use a sun or polarized skylight compass, are able to return directly to their home after a long sinuous outward path (Wehner & Wehner, 1986).

Contrarily to what could be inferred from the flow diagrams provided by Mittelstaedt & Mittelstaedt (1982) and Gallistel (1990), animals obviously do not perform path integration by applying the mathematically correct formulas, but by implementing an approximate although robust neural computation. This led Müller & Wehner (1988) to claim that the path integration mechanism actually used by animals should be described by approximate, simpler, equations. In fact, the approximate solution which is actually implemented by the neural system of an animal to solve a given task is likely to be independent of the complexity of its mathematical formulation. Indeed, mathematical formulas, whether correct or approximate, are very useful tools to represent a given mechanism, but they must not be considered as being the mechanism itself. Modelling path integration has been well served by mathematical formulations. It seems now to be the time to develop path integration models based on plausible neural computation.

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REFERENCES


